DURATION OF LEAVES IN EVERGREENS

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While the duration of leaves in evergreens is not at all a new subject, very little systematic work seems to have been done toward determining durations for an extended list of evergreen species. This work was begun for the purpose of determining the leaf duration of the evergreen species of trees and shrubs in western Washington. It soon developed that the work would not be a mere cataloging of species with their accompanying leaf durations, since a very superficial examination of some of the coniferous evergreens growing under different conditions on the University campus, showed a wide but constant difference in the duration of their leaves. It was then decided to limit the species discussed to those growing under varying conditions that could be examined in the field, and to ascertain, if possible, the factors governing the duration of their leaves.

The Pacific northwest is peculiarly an evergreen region. Sargent (15) described the characteristic coniferous forests as the most luxuriant if not the most diversified on the continent. His report in the Tenth Census states that "Washington is covered with the heaviest continuous belt of forest growth in the United States. This magnificent coniferous forest extends over the slopes of the Cascade and Coast ranges, and occupies the entire drift plain surrounding the waters of Puget Sound." Evergreenness is not only characteristic of the forests, but is equally typical of the forest undergrowth, and of a large list of herbaceous species of the open fields. This is especially true of the Puget Sound region, in which the mild climate affords a practically continuous growing season. This may be one reason why many species elsewhere deciduous are here evergreen.

There are, in the state of Washington, according to Frye and Rigg (2), 76 species of woody evergreens, 24 of which are gymnosperms, and 52 angiosperms. In western Washington there are 52 species, 16 of which are gymnosperms, and 36 angiosperms. Of these the writer has studied the following 9 gymnosperms and 22 angiosperms:

Gymnosperms

1. *Abies grandis*
2. *Juniperus scopulorum*
3. *Picea sitchensis*
4. *Pinus contorta*
5. *Pinus monticola*
6. *Pseudotsuga taxifolia*
7. *Taxus brevifolia*
8. *Thuja plicata*
9. *Tsuga heterophylla*

Angiosperms

(*a*) *Transitional Forms.*—Those species which are deciduous under certain conditions and under others partly evergreen.

10. *Rhamnus purshiana*
11. *Vaccinium parvifolium*

(*b*) *Sub-evergreens.*—Those holding the leaves of one season only until the leaves of the next season are able to carry on the photosynthetic work of the plant. These species are not noticeably affected by external conditions.

12. *Arbutus menziesii*
13. *Ceanothus velutinus*
14. *Linnaea americana*
15. *Micromeria douglasii*
16. *Rubus laciniatus*
17. *Rubus pedatus*
18. *Rubus ursinus*

(*c*) *True Evergreens.*—Species which usually hold their leaves longer than the second season. These are noticeably affected by external conditions.

19. *Arctostaphylos tomentosa*
20. *Arctostaphylos uva-ursa*
21. *Berberis aquifolia*
22. *Berberis nervosa*
23. *Chimaphila menziesii*
24. *Chimaphila umbellata*
25. *Gaultheria shallon*
26. *Kalmia polifolia*
27. *Ledum groendlandicum*
28. *Oxycoccus oxycoccus intermedius*
29. *Pachistima myrsinites*
30. *Rhododendron californicum*
31. *Vaccinium ovatum*

Stark (16), in 1876, spoke of leaf duration as "not a new subject," yet at the same time declared his inability to find anything bearing on the subject in botanical literature. He made extensive observations on the native and introduced conifers in his large private grounds in the British Isles, and distinguished between true leaf fall, as shown in Taxus and Abies, and the shedding bodily of twigs (cladoptosis) as shown in Thuja, Pinus, and *Sequoia sempervirens*. He also remarked that old trees of Picea and Abies held their leaves for a shorter time than saplings.

Legget (10), in 1876, recognized the influence of climate on leaf duration especially in transitional forms.

Hoffman (7), for a series of years prior to 1878, carried on investigations with angiosperm evergreens in the Botanical Gardens at Giessen. He tied tinfoil tags to the petioles of six or eight leaves on a given plant and observed these individual leaves at stated intervals, reporting for several species the leaf duration in months. The method was too cumbersome to be applied on a very large scale, therefore his general conclusions seem hardly justified.

Kraus (8), in 1880, published on the duration of evergreen leaves. Unfortunately his work was not accessible to the writer.

Other writers, as Copeland (1) and Groom (4), also speak of leaf duration. Galloway (3), in 1896, enumerates various factors which may affect leaf duration in *Pinus virginiana;* but these references are all incidental, and mentioned in connection with other problems, or in general descriptions.

Sargent (13) (14) and Sudworth (17) in their descriptions of North American and Pacific Coast trees mention the leaf duration of many species, but their figures do not hold in some cases for the regions under discussion, and they give no estimates for other species which are quite common in this region.

The method of determining the age of a given leaf was simple. In those species having covered buds, the scars marking the boundaries of annual growth made it easy to count the years. In those species with naked buds, as *Thuja plicata* and *Juniperus scopulorum*, freehand sections were made through the twig at the base of the given leaf, and the annual growth-rings of the twig counted under the hand lens or low power of the compound microscope. This method was also used as a check in other doubtful cases.

When counting by means of terminal bud scars, the endeavor was to make counts of 100 twigs, but that was not always possible. In no case, however, did the count fall below 65. When counting by means of sections the attempt was made to obtain counts of 50 twigs. This was done in a majority of cases, and in no case did the count fall below 24. These counts were made in the field whenever possible; or the material was collected and carried to the laboratory, where the counts were made immediately, before handling dislodged leaves, or the unaccustomed dryness of the atmosphere caused them to fall. The counts were afterwards tabulated, and the tabulations placed on a percentage basis, the percent being calculated to the nearest whole number. Finally, curves were plotted from these data (*figs. 1–13*),

the vertical axis representing the percent of twigs or branches examined which bore leaves persisting for the time in years denoted on the horizontal axis.

In making observations on gymnosperms, three chief points were considered on each twig or branch: (*a*) the year in which leaf fall commenced; (*b*) the year of maximum fall, that is, the time when the twigs were fully half bare; (*c*) the extreme duration of the last scattered leaves. In angiosperm species it was considered sufficient to make but one count for each twig or branch, and that to determine the age of the oldest persisting leaf.

The factors considered as having an influence on leaf duration were age of the tree, light, climate, and exposure to constant winds. When studying gymnosperms, observations were made on mature trees growing in the open and in close stands, as well as on saplings growing in the open and under the forest cover. In angiosperm species, observations were made from specimens growing in the open and under the forest cover. The observations included natural gymnosperm forest, partially cleared land, and second growth stands. These observations were made in the vicinity of Seattle, where the winds are not strong and the annual rainfall is about 36 inches.

In order to get contrasting climatic conditions, the writer spent the summer of 1915 at the Puget Sound Marine Station at Friday Harbor on San Juan Island, Washington. This island is sheltered by the Olympic Mountains, leaving the island an annual rainfall of less than 25 inches. The south slopes of the island are wind-swept, the trees having the characteristic one-sided form common to such regions. On this island the Seattle observations were repeated. Also observations were made to see if leaf duration varied in the same species on the leeward and windward slopes.

Several peat bogs in the vicinity of Seattle gave opportunity also to observe the effect of bog habitat on leaf duration. The observations were made partly at the bog one-half mile east of Ronald, Washington; partly at the Mud Lake bog, near the west shore of Lake Washington at 65th St., Seattle.

Since leaf duration varies with the conditions under which the plant is growing, and since these conditions are matters of general observation rather than of accurate measurements, it follows that the results are general. The longest durations are for the poorest combination of conditions; the shortest duration for the best combination

of conditions; and the average duration merely the average of these conditions as nearly as could be ascertained from all the observations made. Mere general observation of the external and internal conditions of tree are not sufficiently accurate to enable one to predict with certainty just what one will find in a given tree.

1. *Abies grandis* Lindl. Shortest leaf duration observed, 2 years; average, 4–10 years; extreme, 14 years. All observations were made in the San Juan Islands, since the species is rare in the vicinity of Seattle. Old trees have a longer leaf duration than do saplings; shade tends to increase leaf duration; the leaves of wind-swept trees have a shorter duration than those of protected trees (*figs.* 9, 10).

2. *Juniperus scopulorum* Sarg. Shortest duration of green color observed, 1 year; average, 2–3 years; extreme, 4 years. The leaves, however, persist after turning brown. This results in the following: shortest leaf duration, 3 years; average, 4–6 years; extreme, 14 years. West of the Cascades this species occurs at low altitudes only in arid regions. It is quite common in the San Juan Islands. Two distinct types of leaves are found. The juvenile type, which are long, awl-shaped, and spreading, have a shorter duration than the adult, overlapping scale-like type. In all cases observed, the leaves lost their green color from 1–4 years before they fell, and were then gradually sloughed off.

3. *Picea sitchensis* Traut. & May. Shortest leaf duration observed, 2 years; average, 9–11 years; extreme, 18 years. In the vicinity of Seattle this species was observed only in peat bogs. In the San Juan Islands the trees observed stand at the head of a salt marsh which extends up a creek bed from False Bay. Mature trees in ordinary soil were not available and no saplings were observed, so that the results given are by no means complete.

4. *Pinus contorta* Dougl. Shortest leaf duration observed, 2 years; average, 4–6 years; extreme, 9 years. Leaf duration reported by Sargent (13), (14), 7–8 years; by Sudworth (17), 6–8 years. In the San Juan Islands, saplings in the open, and mature windswept trees, showed the shortest leaf duration; mature trees, protected from the wind, the longest duration. Trees introduced on the University campus showed the shortest duration observed. Sudworth states that "long persistence appears to belong more to young trees," but the writer found the opposite to be true.

5. *Pinus monticola* Dougl. Shortest leaf duration observed, 1 year;

average, 3–4 years; extreme, 6 years. Leaf duration reported by Sargent (13), 3–4 years. This species, found commonly in the Puget Sound region in peat bogs, showed the shortest duration of any of the gymnosperms studied. Mature trees show a tendency to hold their leaves longer than do saplings.

6. *Pseudotsuga taxifolia* Britton. Shortest leaf duration observed, 1 year; average, 3–9 years; extreme, 16 years. Leaf duration reported by Groom (4), Sargent (14) and Sudworth (17), about 8 years; by Ward (19), 6–7 years. Observations showed that saplings have a much shorter leaf duration than do mature trees; trees in the open have a much shorter leaf duration than those in the shade; wind-swept trees have a short leaf duration; a dry climate increases leaf duration; a peat bog habitat increases the duration of leaves in saplings to a greater degree than does a dry climate. No observations were made on mature trees in peat bogs. A winter season of unusual severity, such as that experienced by the Pacific northwest in January and February, 1916, when snow lay on the branches for several weeks, seriously affects the duration of the leaves. Thirty-eight percent of the branches examined showed partial loss of the leaves of the preceding season's growth, whereas no such loss was observed on the same trees during the same period of the preceding year. It was noted also that, in specimens of *Pseudotsuga taxifolia* growing in dense shade, the annual thickening of the trunks was very slight, the leafy twigs were very slender, and the needles small and comparatively few on a year's growth (*figs*. 1–5).

7. *Taxus brevifolia* Nutt. Shortest leaf duration observed, 2 years; average, 5–12 years; extreme, 23 years. Leaf duration reported by Sargent (14), 4–5 years; by Sudworth (17), 6–9 years.

A summary of the effects of varying external conditions cannot be given since not enough data could be secured. However, in ordinary conditions of moisture for the Puget Sound region, and in densely shaded locations in the drier climate of the San Juan Islands, the duration of leaves has been found to be much greater than previously supposed.

8. *Thuja plicata* Donn. Shortest duration of green color, 1 year; average, 2–5 years; extreme, 7 years. Since the leaves persist after losing their color the duration is longer than given above. Observations resulted in the following: shortest leaf duration observed, 3 years; average, 4–7 years; extreme, 12 years. Leaf duration reported by

Sargent (14) and Sudworth (17), about 3 years. Observations seem to indicate that the leaves of mature trees have a greater duration than those of saplings; that leaves in the shade have a greater duration than those in the open; that a dry climate seems to prolong the duration of the leaves; that a bog habitat has the same effect as a dry climate. Leaves remain on the tree for at least two or three years after losing their green color, and then are gradually sloughed off by the increase in size of the twig. Sudworth and Sargent also agree in saying that the lateral branchlets, which are shed entire, fall in their second year. The writer found that the duration of lateral branchlets also varies with habitat. Full data were not taken, but observations showed that under typical moisture conditions their duration was 2 to 3 years, while in bog specimens they persisted 4, 5 or 6 years (*figs.* 11, 12).

9. *Tsuga heterophylla* Sarg. Shortest leaf duration observed, 2 years; average, 4–7 years; extreme, 12 years. In general, mature trees show a greater leaf duration than do saplings under the same conditions of light and moisture. However, the shaded saplings observed in the vicinity of Seattle showed a greater leaf duration than that of mature trees growing under the same conditions. The saplings observed grew on fallen logs in dense shade under the parent trees, and had grown very slowly. Specimens which showed 20 annual growth-rings were less than a meter high, and no thicker than an ordinary lead pencil. The linear growth per year in many of the twigs examined was less than a centimeter, the needles on each year's growth were few in number, and the individual leaves were very small. There may be some correlation between this extreme slowness of growth and the increased duration of the leaves. Saplings in a moist climate show a longer leaf duration than saplings in a dry climate, while the converse is true for mature trees.

Bog saplings, observed in the peat bog at Ronald, Washington, were dwarfed and stunted in their growth to a much greater extent than the shaded saplings previously described. As determined by counting the annual rings under the low power of the compound microscope, these saplings ranged in age from 5 to 32 years. They were from 17 to 60 cm. high, but the height was not proportional to the age. Both lateral and terminal shoots averaged less than a centimeter per year in linear growth; and a year's growth in many cases comprised from 6 to 10 needles, which were much below normal in size. The leaf durations in these bog saplings show a remarkable feature, which

was not observed in the case of any other species examined, under any condition. All three curves, that is, for beginning of leaf fall, for maximum leaf fall, and for extreme duration, show two maxima, the first occurring in the fourth year in all three cases, and the second in the sixth and seventh. This is probably due to variations in the toxicity of the bog water in different parts of the bog (13). Mature specimens from the bog also showed slow growth and small needles, but the duration curves were normal and the maxima lay between the two sets of maxima in the curves of the saplings. Peat bog specimens, both saplings and mature, show an increased leaf duration over specimens growing in the open in ordinary soil, the duration more nearly approximating that of specimens from a drier climate (*figs*. 6–8).

10. *Rhamnus purshiana* DC. Sudworth says that "in its northern habitat the thin large leaves are shed regularly in the autumn, while in the drier southern distribution to and through central California, the leaves, which are smaller, thicker, and somewhat leathery, often persist more or less during late autumn and winter." Frye and Rigg (2) state that the leaves are "deciduous except occasionally on very young plants." Sargent (14) says that "in Washington and Oregon the leaves fall late in November, while farther south and near the California coast they remain on the branches almost all winter, or until the following spring." The writer has found that not only do seedlings retain their leaves in the Puget Sound region, but that trees in moist rich humus under the forest cover, up to ten years old, may retain at least a part of their leaves well on into May, when the new season's leaves are fully expanded; and these persistent leaves seem not to differ in size or texture from those shed in the fall.

11. *Vaccinium parvifolium* J. E. Smith. The small plants which have germinated on fallen logs under the forest cover are almost invariably evergreen. The slender branches which arise from the root crowns of older shrubs also bear leaves which persist from one to several seasons. It was thought at first that evergreenness was confined to branches near the ground, but later several specimens were found which bore evergreen leaves from 1 to 2 meters above the ground, on the upper branches. Two distinguishing characteristics present themselves in regard to these evergreen leaves:

(*a*) The leaves are usually much smaller than the ordinary deciduous leaves, and are borne on very slender, slow-growing branches.

These branches attain a growth usually of less than 5 centimeters in a season, and may bear no more than 3 leaves on a season's growth. However, leaves of 3 or 4 years' growth have been found which were from 20 to 30 mm. in length, while the species description, Frye and Rigg (2), gives leaves 6 to 17 mm. long.

(*b*) While evergreen leaves are quite common, they are not usual on mature shrubs, and there seem to be no definite external factors which will explain their appearance or non-appearance. At best, only a few branches bear evergreen leaves. Also, of two shrubs of approximately the same age, growing under apparently the same conditions, and standing only 3 or 4 meters apart, one may be entirely devoid of leaves and the other have several branches bearing leaves of 3, 4, 5 or even 6 years' duration. The extreme duration observed was 6 years.

12. *Arbutus menziesii* Pursh. Observations were made on the campus of the University of Washington. The leaves begin to fall early in June of their second year. Many of the trees put on a second growth late in the summer, whose leaves are somewhat smaller and lighter in color than the normal spring leaves, and this gives the appearance of two seasons' growth. During the extreme and unusual cold weather of the past winter, many of the spring leaves were killed by frost while the late summer leaves seemed to be scarcely affected. This enhances still more the appearance of two seasons' growth.

13. *Ceanothus velutinus* Dougl. Like *Arbutus menziesii*, this normally holds the leaves of one season only until those of the succeeding season are fairly matured; that is, for a period of about 15 months.

14. *Linnaea americana*, Forbes. This trailing vine, as a rule, does not drop its leaves, but the leaves simply decay while attached, as they lie against the damp moss or already decaying leaves of the substratum. They persist throughout the winter, and in many cases until after the flowering season in the spring.

15. *Micromeria douglasii*, Benth. The same condition is found in this as in *Linnaea americana*.

16. *Rubus laciniatus* Willd. This plant has escaped from cultivation, and is commonly known as the "evergreen blackberry." Some leaves persist at least until after the flowering season.

17. *Rubus ursinus* Schlecht. & Cham. This is common on logged-off lands; according to Frye and Rigg (2) it is evergreen only in western Washington.

18. *Rubus pedatus* J. E. Smith. The writer found a single specimen, and that bore leaves of two seasons' growth.

19. *Arctostaphylos tomentosa* Dougl. The writer had access to only one specimen, a shrub which has stood for several years in the northwest angle of a 3-story building on the University campus. This showed a leaf duration of 4, 5 and 6 years on various branches.

20. *Arctostaphylos uva-ursa* Spreng. Shortest leaf duration observed, 2 years; average, 3 years; extreme, 5 years.

21. *Berberis aquifolium* Pursh. Shortest leaf duration observed, 1 year; average, 2–4 years; extreme, 6 years. Not found usually in shaded situations. A dry climate shortens its leaf duration.

22. *Berberis nervosa* Pursh. Shortest leaf duration observed, 2 years; average, 3–4 years; extreme, 8 years. Plants growing in the shade show a longer leaf duration than those growing in the open. A dry climate accents the difference in duration between leaves in the open and those in the shade.

23. *Chimaphila menziesii* Spreng. Shortest leaf duration observed, 2 years; average, 4–5 years; extreme, 8 years. This species was found only in a limited area on San Juan Island.

24. *Chimaphila umbellata* Nutt. Shortest leaf duration observed, 1 year; average, 2–4 years; extreme, 7 years. A dry climate tends to increase its leaf duration.

25. *Gaultheria shallon* Pursh. Shortest leaf duration observed, 1 year; average, 2–4 years; extreme, 6 years. Shade plants under typical moisture conditions have a shorter leaf duration than plants in the open, while under dry conditions plants in the open have the shorter leaf duration. Plants growing in sphagnum about the margins of peat bogs resemble in growth-habit plants growing in the open in ordinary soil, but have a decided tendency toward shorter leaf duration.

26. *Kalmia polifolia* Wang. Shortest leaf duration observed, 1 year; average, 2 years; extreme, 3 years. In contrast to Ledum, shaded plants showed a tendency to shorter leaf duration, and plants which had been growing for several years in the experimental gardens were entirely bare of leaves when observed in December.

27. *Ledum groenlandicum* Oeder. Shortest leaf duration observed, 1 year; average, 2–4 years; extreme, 5 years. Plants in an open peat bog showed the shortest leaf duration. Plants which had been transferred to the experimental gardens of the university campus several years ago showed a marked tendency to increased leaf duration.

Plants growing in the shade about the borders of the bog were much modified, being much taller; and with leaves larger, thinner, less revolute, and less densely clothed with hairs on the under surface. These leaves were of much longer duration.

28. *Oxycoccus oxycoccus intermedius* Piper. Shortest leaf duration observed, 1 year; average, 2–3 years; extreme, 4 years. Plants partially shaded by the taller growth of Ledum about the hemlock hillocks showed increased leaf duration.

29. *Pachistima myrsinites* Raf. Shortest leaf duration observed, 2 years; average, 3–4 years; extreme, 8 years. This species was observed only in the San Juan Islands. Plants growing in exposed locations on the windward side of the islands had a shorter leaf duration than those on the leeward side.

30. *Rhododendron californicum* Hook. Shortest leaf duration observed, 1 year; average, 2 years; extreme, 3 years. This plant was observed only on the university campus, where it is used extensively as an ornamental shrub.

31. *Vaccinium ovatum* Pursh. Shortest leaf duration observed, 2 years; average, 2–4 years; extreme, 7 years. Plants in the shade show a decided increase in leaf duration (*figs.* 13).

It has already been noted that in many of the gymnosperms growing under adverse conditions, that is, in dense shade or in peat bogs, leaves are smaller and fewer in number on a year's growth than on specimens of the same species growing under more favorable conditions. While the tendency is not so marked in all cases the same difference in size was noted between the leaves of mature trees and those of saplings, mature trees ordinarily having smaller leaves than those of saplings.

Kraus (9) observed that the length and vigor not only of the growing shoots but also of the needles vary in different seasons; and Reinke (12) demonstrated that in transplanted evergreens the needles formed during the growing season immediately following the transplanting are conspicuously shorter than those formed during either the preceding or the following season. This was afterward confirmed by Copeland (1), who measured the needles on transplanted evergreens on the campus of Indiana University. Former observations are thus extended to include the variation in size of leaves on trees of the same species of different age, or growing in different habitats.

Groom (5) observed that though the individual leaf is small, the aggregate leaf surface of the conifer often greatly exceeds that of the

dicotyledonous tree; and Copeland (1) in his study on the size of evergreen needles found that in abnormal years, when the leaves are small, "the number of needles compensates the plant for their lack of size, sometimes furnishing an even greater surface of leaf than is borne on the normal year's growth of stem." Following the same line of thought, it may be that the longer duration of leaves on mature trees, or on trees growing under adverse conditions, which is correlated with a decrease in size, tends to keep up the total leaf area. With longer duration and smaller leaves in dense shade as compared with open situations, increased duration may be correlated with two factors. Reduced size of the individual leaf, and reduced photosynthetic activity, due to diminished light intensity, are both compensated by an increased number of leaves; and increased leaf duration would furnish this increase in the number of leaves.

In all angiosperm forms which were examined, both in the open and in the shade, the leaves on shaded plants were much larger than those on plants exposed to direct sunlight; and with the exception of *Gaultheria shallon* growing in the typical climatic conditions of the vicinity of Seattle, plants in the shade held their leaves longer than those in the open. Hasselbring (6), in commenting on his experiments with Cuban tobacco grown under a cheese-cloth shade, states that "the reduction in photosynthesis in the shade leaves was compensated by an increase in leaf area, so that the production was not diminished." In various species under discussion, it is quite possible that the increase in photosynthetic area, which compensates the decrease in light intensity, is due not only to the increased size of the leaves but also to their increased duration.

Conclusions

1. Leaf duration varies widely among the different evergreen species, ranging from *Rhamnus purshiana*, which in young plants sometimes holds part of the leaves of one season until those of the next season are mature, to *Taxus brevifolia*, which has an extreme leaf duration of 23 years.

2. Leaf duration varies widely in individuals of the same species of different age or growing in different habitats: (*a*) Saplings have a shorter leaf duration than mature trees in the same habitat. (*b*) Trees or shrubs growing in the open have a shorter leaf duration than those of similar age in the shade. (*c*) Trees or shrubs on a windward coast have a shorter leaf duration than those on a leeward coast. (*d*) Gym-

nosperms in a moist climate have a shorter leaf duration than those in a drier climate. (*e*) A peat bog habitat has an effect similar to a dry climate.

3. Those factors which cause slowness of growth, and thus only a slight increase in diameter of the axis, are accompanied by an increased duration of the leaves.

4. Under the same climatic conditions, those factors which cause an increase in transpiration are accompanied by a decrease in leaf duration, and thus by a decrease in the transpiring surface.

5. Those factors which cause a decrease in photosynthetic activity are accompanied by an increase in leaf duration, and thus by an increase in the photosynthetic area.

6. It is quite possible that the variations in leaf duration in a given species may be due to differences in transpiration or photosynthetic activity, caused by difference in age or habitat.

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EXPLANATION OF FIGURES 1-13

Horizontal figures indicate years; vertical figures indicate number of specimens. Unless otherwise stated, ... is curve showing beginning of leaf fall; ——is curve showing greatest leaf fall; - - - - is curve showing extreme duration of leaves.

FIG. 1. *Pseudotsuga taxifolia*, on San Juan Island; mature trees, in the open, on leeward slope.

FIG. 2. *Pseudotsuga taxifolia*, at Seattle; sapling, in the open.

FIG. 3. *Pseudotsuga taxifolia*, at Seattle; mature tree, in the open, after unusually cold weather.

FIG. 4. *Pseudotsuga taxifolia*, on San Juan Island; mature tree, in the open, on windward slope.

FIG. 5. *Pseudotsuga taxifolia*, at Seattle; mature tree, in the open.

FIG. 6. *Tsuga heterophylla*, at Seattle; mature tree, in peat bog.

FIG. 7. *Tsuga heterophylla*, on San Juan Island; mature tree, in the open.

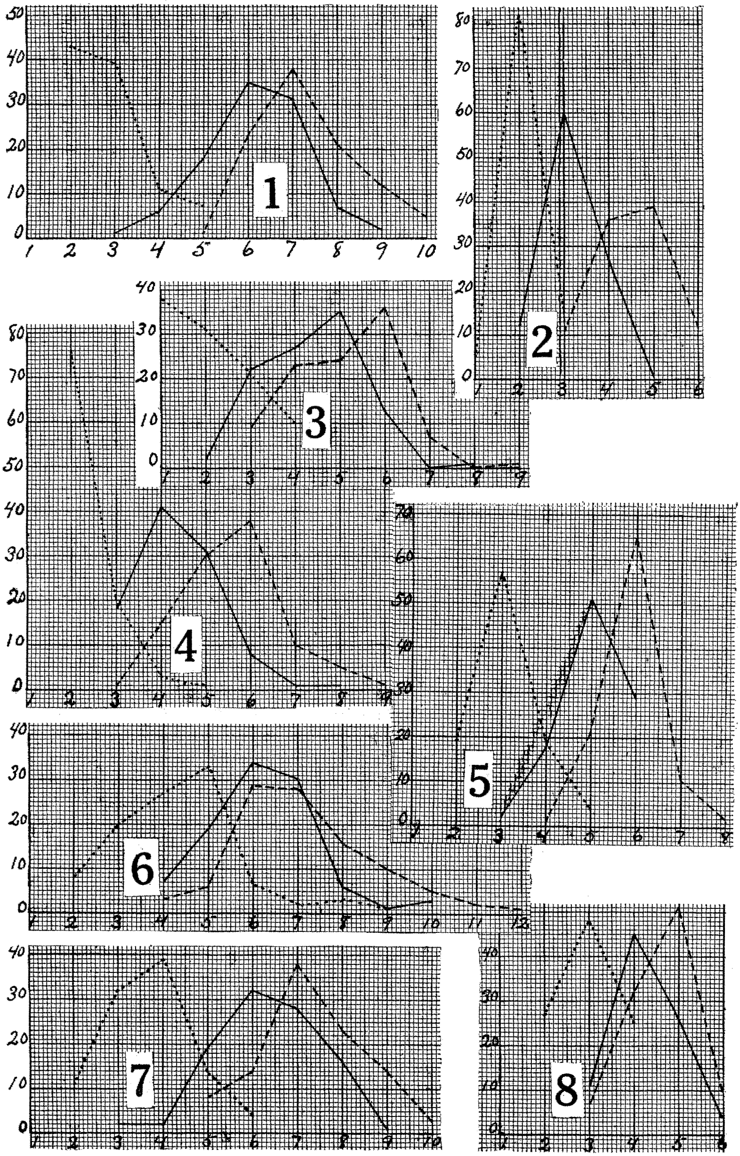
FIG. 8. *Tsuga heterophylla*, at Seattle; mature tree, in the open.

FIG. 9. *Abies grandis*, on San Juan Island; sapling, in the shade.

FIG. 10. *Abies grandis*, on San Juan Island; sapling, in the open.

FIGS. 11 AND 12. *Thuja plicata*, on San Juan Island; mature trees; Fig. 11 in the shade, Fig. 12 in the open. ...... is curve of loss of green color; —— is curve of beginning of leaf fall; - - - - is curve of extreme leaf duration.

FIG. 13. *Vaccinium ovatum*, at Seattle. —— is curve of extreme leaf duration in shade; - - - - is curve of extreme leaf duration in open.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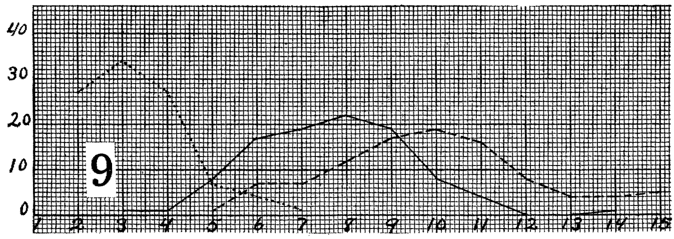
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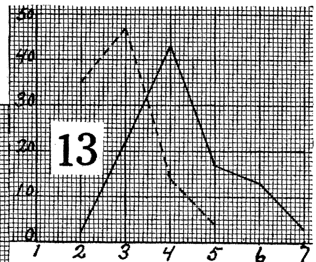
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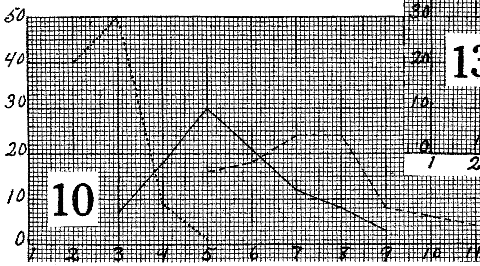
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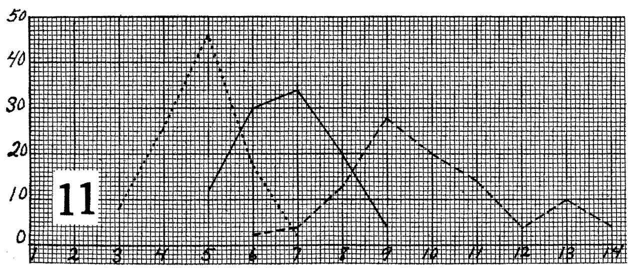
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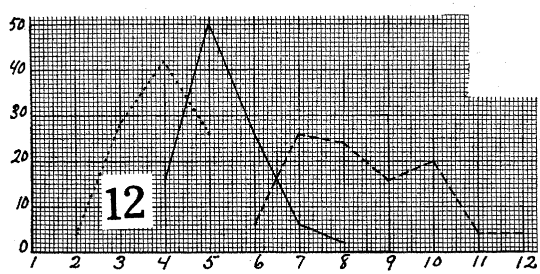
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